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TWO FUNGUS DISEASES OF THE WHITE CEDAR.

BY JOHN W. HARSHBERGER, PH.D.

PREFATORY REMARKS.

The white cedar is a stately tree seventy to eighty feet in height, and one to four feet in diameter. It lives in the cold sphagnum swamps of the Atlantic and Gulf coast plains, where frequently the bases of the tree are flooded with water. In New Jersey, and in the North generally, it forms an almost pure growth. It is associated in the South with the bald cypress, *Taxodium*. Extending from southern Maine along the coast to northern Florida and then westward to the Pearl river in Mississippi, it never is met with far inland, being confined almost entirely to the coastal plains.

The tree is not subject to any very serious disease. It is remarkably exempt from both insect and fungal enemies, and consequently it should be looked upon as a promising tree for future systematic forestry in the eastern United States. It gives value to lands that without it would be useless. Sydow¹ gives nineteen species of fungi living on *Cupressus thyoides*. To this number one additional fungus should be added, viz., *Gymnosporangium Ellisii* Berk. Of these, ten species are found growing on the leaves, causing no material injury to them, as the fungi are usually found on dead leaves. Five fungi are confined to the branches, one is found on the trunk, two grow on the bark, two are found on the wood and one fungus, *Gymnosporangium biseptatum*, occurs on both leaves and branches. The majority of these fungi are saprophytes living on the dead parts of the white cedar. Only two fungi may be called disease-producing, viz., *Gymnosporangium biseptatum* Ellis and *Gymnosporangium Ellisii* (Berk.) Farlow.

The latter species, *Gymnosporangium Ellisii*, was first described by

¹ SYDOW, *Index Universalis et Locupletissimus Nominum Plantarum Hospitium Specierumque Omnium Fungorum*, 1898, p. 375.

Berkeley² as *Podisoma Ellisii*. Farlow³ transferred the species to the genus *Gymnosporangium*, and gave somewhat in detail the external appearance of the witches' brooms caused by the growth of the fungus. It causes a fasciation of the smaller branches of the white cedar, which become more or less fan-shaped brooms. The external portion of the fungus is smaller and less gelatinous than in any other species of the genus. Sargent, in the *Silva of North America*, enumerates in a footnote (X, p. 100) the more important fungi that live on the true cedars, mentioning *Gymnosporangium Ellisii* (Berk.) Farlow and the following parasitic plant, *G. bisep-tatum* Ellis, as of most importance from a pathological standpoint.

HISTORICAL.

The fungus *Gymnosporangium bisep-tatum* was first described by Ellis⁴ in the following words: "On branches of white cedar. Appearing in April, bursting through the epidermis in little reddish chestnut-colored velvet-like patches which, about the middle of May, pass into the tremelloid state, swelling out into gelatinous masses the size of large peas; not so distinctly foliaceous as in *G. juniperi*. Spores long pedicellate, mostly bisep-tate." Ellis, also in this place, referred to the appearance of the swellings produced by the fungus. Farlow⁵ studied and described the fungus in a more thorough manner, but his account has largely to do with the botanical characters of the plant, the external appearance of the swellings and the variation of the spores. He referred in a casual manner to the fact that "the mycelium is found principally in the region of the cambium." Sorauer⁶ described somewhat carefully in detail the life-history of the *Gymnosporangia* and their corresponding *Ræstelia*. As the basis of his remarks, he took *Gymnosporangium fuscum* and *Ræstelia cancellata*, described the botanical characters of both the teleutosporic stage and the æcidio-sporic stage, and referred briefly to the other common species of the genus, viz., *Gymnosporangium clavariæforme*, *G. conicum*, *G. mac-ropus*, *G. bisep-tatum*, *G. tremelloides*, *G. Ellisii*. Wörnle⁷ inves-

² BERKELEY, *Grevillea*, III, p. 56.

³ FARLOW, *Bulletin Bussey Institute*, II, p. 226: The *Gymnosporangia* or Cedar Apples of the United States, 1880.

⁴ ELLIS, *Bulletin Torrey Botanical Club*, 1874, V, p. 46.

⁵ FARLOW, The *Gymnosporangia*, etc., pp. 19-20.

⁶ SORAUER, *Pflanzenkrankheiten*, 1886, II, pp. 232-239, taf. X.

⁷ WÖRNLE, Anatomische Untersuchung der durch *Gymnosporangien*-Arten hervorgerufenen Missbildungen. "Inaugural Dissertation." *Bot-anisches Centralblatt*, 1894, LX, pp. 280-283.

tigated more particularly the pathological symptoms produced in the host plants by the European species of *Gymnosporangium*, viz., *G. juniperinum*, *G. clavariæforme*, *G. sabinae*, and in a general way, with imperfect material at his disposal, the pathology of the American species of *Gymnosporangium*, viz., *G. Ellisii*, *G. biseptatum*, *G. clavipes*, *G. macropus*. He investigated the changes produced in the bast, the cortex and the wood of *Juniperus nana* and *J. communis* by *Gymnosporangium juniperinum* (*conicum*); of *J. communis* by *G. clavariæforme*; of *J. sabina* by *G. sabinae*. He investigated in a most general manner the disease conditions induced by the American species of this genus of fungi. Hartig⁸ described the botanical characters of the following species of *Gymnosporangium*: *G. conicum* (*juniperinum*), *G. clavariæforme*, *G. sabinae* (*fuscum*), *G. tremelloides*. Frank⁹ described in a general way the botany and pathology of *Gymnosporangium fuscum*, *G. confusum*, *G. clavariæforme*, *G. conicum*, *G. Ellisii*, *G. macropus*, *G. biseptatum*, *G. clavipes*, *G. globosum*, *G. nidus-avis*, *G. Cunninghamianum*. Plowright¹⁰ obtained some unexpected results by cultures made with the teleutospores and æcidiospores of the three European species of *Gymnosporangia*, viz., *G. clavariæforme*, *G. conicum*, *G. fuscum*, enlarging materially the list of plants upon which the Ræstelia of these plants are found. Thaxter,¹¹ by numerous culture experiments, succeeded in most cases in working out the life-histories of the American species of the genus *Gymnosporangium*, by connecting the æcidial stage on rosaceous plants with the teleutospore stage on various coniferous trees. Sanford¹² studied the structure of the twigs of the red cedar with reference to the formation of the cedar apple. He made a detailed microscopic study of the cedar apple swelling, the spores and the spore-bearing filaments. A brief mention of these articles is sufficient to draw attention to the fact that very little work has been done on the pathological conditions produced by the American species of *Gymnosporangium*.

⁸ HARTIG, *The Diseases of Trees* (English translation), 1894, p. 157.

⁹ FRANK, *Die Pilzparasitären Krankheiten der Pflanzen*, 1896, II, pp. 176-184.

¹⁰ PLOWRIGHT, British Heteræcious Uredines, *Journ. Linn. Soc. Bot.*, 1888, XXIV, p. 93.

¹¹ THAXTER, *Bot. Gaz.*, 1889, XIV, p. 163; *Conn. State Exper. Stat. Report*, 1891, p. 161.

¹² SANFORD, *Annals of Botany*, 1887, I, p. 263.

The attention of the writer was drawn to the swellings a year or two ago, while botanizing in the coastal plain of New Jersey. Specimens of the swellings caused by the two fungi were collected in a cedar swamp at Island Heights Junction, N. J. Both the fanlike growth of the younger branches and the larger knotty growths on the older branches and the trunk of the trees were met with in this cedar swamp. The large knob-like swellings, a foot or more in diameter, girdling the trunk of large trees, were seen in a cedar swamp at Newfield, N. J.

METHODS.

Sections of the swellings caused by *Gymnosporangium bisepatum* were made by means of a plane. The smaller sections were mounted in the usual way on slides, and the larger sections were mounted on window glass with thinner pieces of white glass as covers, and these preparations were then placed over a steam radiator until the balsam was perfectly dry and hard. The covers were kept in place during the drying by spring-clip clothes pins, which suited the purpose admirably. Bismarck-brown, aniline-green and an admixture of acid-fuchsin and methyl-green were used with satisfactory results in the demarcation of the tissues.

APPEARANCE OF THE SWELLINGS.

The swellings produced by *Gymnosporangium bisepatum* Ellis are quite characteristic. The disease may appear on trees which are from five to six feet high, with stem about an inch in diameter. In these young trees the swelling surrounds the whole stem, being about three inches long and approximately spindle-shaped (Pls. XXII, XXIII, figs. 1, 2, 3, 4, 5). The bark is deeply fissured by longitudinal cracks, which are also somewhat wrinkled at the bottom (fig. 3). In a stem three-eighths inch diameter, the wood involved is quite sound, although in dried specimens of a more decided yellow color than the wood of the stem below, which is whitish in color. As the mycelium of the fungus is perennial, these club-shaped enlargements keep constantly increasing in length and diameter from year to year. In another somewhat larger specimen studied, the burl reaches a diameter of an inch and a half and is about six inches long. The fissures become much deeper, due to

the abnormal formation of the cork, until on one side of the stem the bark ridge is one-half inch high, the groove being correspondingly deep. These ridges of bark covered with small lichens give to the swelling an extremely rough, cancer-like appearance (fig. 5). The wood assumes a brownish aspect and the annual rings, as seen by the naked eye, are more or less wavy. Occasionally the malformation appears as an enlarged excrescence. It would seem that this excrescence began its growth upon a young lateral branch, which afterward ceased its elongation and was covered up by the enlarging fungus-infested mass of wood. The burls are about three inches long and about two inches wide, with the bark fissured into deep grooves with rather broad corky flakes. The wood to the naked eye resembles in appearance the well-known curly or bird's-eye maple. In another specimen examined, the swelling seven inches long involves the main stem and one of its branches, so that the swelling, which is fissured in the characteristic way and two inches in diameter, may be said to have forked.

The swellings produced by *Gymnosporangium Ellisii* Berk. are confined to the smaller twigs and branches. Near the summit of young white cedar trees where the branches grow upward, and are thus more or less crowded together, all of these branches may be involved (fig. 8). The result is the formation of fan-shaped mass of swellings, which assume a fasciculate character when closely crowded. The trees attacked by it may, therefore, be recognized, even at a considerable distance by the peculiar distortions, which consist in a dense fasciculation of the smaller branches in different parts of the tree, so that, viewed from a distance, one sees closely branching tufts of a corymbose outline, which appear to terminate some of the branches (fig. 8). On one lateral branch of white cedar, one-half inch in diameter, twelve smaller branches were all massed together into a witches' broom. The external appearance of the bark on these branches is somewhat different from that described for *G. bisepatum*. Here the bark is fissured transversely. With a few longitudinally directed cracks the reddish-brown bark is thus divided into a number of plates, rectangular in shape (fig. 8). The smaller twigs are not thus affected, but instead have a somewhat rugose continuous surface. One or two of the branches involved by the fungus are dead. The swellings differ also from those formed by the preceding fungal species in tapering gradually

from the basal end of the twig, where the swelling is largest, toward the distal end, where the growth merges with the normal diameter of the branch (fig. 8). The abnormalities on the lateral branches of two other young trees of white cedar are marked, because the secondary branches have increased considerably in number and have assumed a fastigiate habit, radiating upward and outward from an approximately common point. As many as twenty small branches, all about six inches long, are to be counted in a single fastigation (fig. 8). The surface of the bark in these specimens is raised into vesicular roughenings, which condition seems to precede the formation of the rectangular plates of bark by some interval of time.

NORMAL STEM STRUCTURE OF WHITE CEDAR.

According to Prof. Sargent,¹³ "the wood of *Cupressus thyoides* is light, soft, not strong, close-grained, easily worked, slightly fragrant, and very durable in contact with the soil. It seasons rapidly and perfectly without warping or checking; it is light-brown tinged with red, with thin lighter-colored sap-wood, but grows darker with exposure, and contains dark-colored, conspicuous narrow bands of small summer-cells, and numerous obscure medullary rays. The specific gravity of the absolutely dry wood is 0.3322, a cubic foot weighing 20.70 pounds."

The sections, made with a hand-plane, were stained with three different stains, viz., methyl-green, Bismarck-brown and a mixture of methyl-green and acid-fuchsin used as a double stain. The histological details of the stem in an undiseased state are as follows: The pith of a twenty-one-year-old stem with wood three-eighths inch diameter is almost entirely absent. Its place is filled by the closely aggregated spiral tracheæ which compose the region known as the protoxylem. From this small contracted protoxylem radiate toward the cortex the primary medullary rays and the wedges of xylem. The medullary rays are numerous, but obscure. They consist in the cross-section of but a single row of thin-walled parenchyma cells which are six times longer than broad. The wedges of wood are narrow, their radial limits being defined by the medullary rays. The following table shows the variation in the size of the annual rings, as determined by a count under the microscope

¹³ SARGENT, *Silva of North America*, X, p. 112.

of the number of tracheids in a single radial line, proceeding from the cambium to the pith. The striking feature in this enumeration

TABLE I.

| Number of Annual Ring. | Year. | Number of Tracheids. | Number of the Tracheids in the Autumn Wood. |
|---------------------------|-------|-------------------------|--|
| 21 | 1900 | 6 | 2 |
| 20 | 1899 | 10 | 3 |
| 19 | 1898 | 21 | 5 |
| 18 | 1897 | 18 | 5 |
| 17 | 1896 | 18 | 4 |
| 16 | 1895 | 15 | 5 |
| 15 | 1894 | 12 | 3 |
| 14 | 1893 | 6 | 1 |
| 13 | 1892 | 16 | 5 |
| 12 | 1891 | 12 | 4 |
| 11 | 1890 | 15 | 4 |
| 10 | 1889 | 12 | 5 |
| 9 | 1888 | 9 | 3 |
| 8 | 1887 | 6 | 2 |
| 7 | 1886 | 7 | 2 |
| 6 | 1885 | 10 | 3 |
| 5 | 1884 | 9 | 2 |
| 4 | 1883 | 10 | 5 |
| 3 | 1882 | 6 | 3 |
| 2 | 1881 | 7 | 3 |
| 1 | 1880 | | |

of the tracheids is the uniformity of the growth (fig. 9). The diameter of the lumen and the thickness of the cell wall in nearly all of the tracheids of the spring and summer wood is very nearly the same in all of the annual rings of wood. This, and the fact that the annual rings are not clearly delimited by the naked eye, and in some cases even with the microscope, argues for an extremely uniform rate of growth. A uniform rate of growth presupposes environmental conditions of little variation.

The factors which influence the growth of the tree and the formation of the wood are, therefore, fairly constant during the growing season, and it is not until near the time of the cessation of growth that a few tracheids of thick walls and narrow lumen are laid down as autumn wood. We would expect just such influencing environmental conditions in a sphagnum bog.

CONDITIONS INFLUENCING THE GROWTH OF WHITE CEDAR
AND ITS PARASITIC FUNGI.

The temperature of sphagnum bogs is well known to be low, and the expression cold bogs is frequently met with in the descriptions in the manuals. European students of bogs consider the low temperature as due to evaporation from the surface of the sphagnum which grows in the bogs, but this seems altogether inadequate to explain the phenomenon. Ganong¹⁴ supposes it to be due rather to a persistence of the winter cold, which in such a non-conducting mass would last through the summer. In this explanation the writer entirely agrees with Prof. Ganong, although in New Jersey the winter cold does not persist throughout the entire summer. One would expect this from the more southern position of New Jersey, as compared with the northern latitude of New Brunswick, there being a difference of six degrees of latitude between the two stations. The difference in latitude hardly expresses the difference in climate, because of the exposure of New Brunswick to the descending polar currents. "It is easy to test these two hypotheses; for if the former be true there should be little change in the temperature conditions after the summer average is once attained, or even the bog might be somewhat lower in temperature when the season is hottest, and hence evaporation most active; if the latter be true the bog should steadily rise in temperature through the summer." Ganong took the temperature of the bogs studied by him and found that there was a perceptible rise of temperature during the summer, the temperature rising in two months an average of 2° at one foot under the surface. The same author found on July 1, near the centre of the bog observed by him, sheets of ice six to eight inches thick and several feet square about a foot under the surface.

All of these facts are of interest in connection with the character of growth of the white cedar. The persistence of the uniform temperature, *i.e.*, the slow heating up of the soil and water of the swamps, regulates to a remarkable degree the character of the annual rings of wood. With rapid growth in the wet spring, ordinary dicotyledonous trees, as a rule, have well-defined spring elements with usually wide open lumen. As the summer advances

¹⁴ GANONG, Upon Raised Peat Bogs in the Province of New Brunswick, *Transactions of the Royal Society of Canada*, 2d Ser., III, p. 151.

and the soil becomes drier and warmer, the xylem elements become thicker walled and the lumen smaller, forming the so-called autumn xylem. Where the spring growth is delayed until growth fairly commences and where the soil and ground water temperature remain almost constant, the tracheids approach a uniform thickness and size. The annual rings are consequently not well characterized, and it requires in many cases a microscopic examination to determine the limits of the rings of wood annually laid down. We have in the white cedar, *Cupressus thyoides*, of the New Jersey bogs an exemplification of this character of ill-defined annual rings due to the influence of the uniform condition of growth. The question may be asked at this point, Why this digression? The answer is, the whole question of growth has a very important bearing on the entrance, growth and spread of the fungi which cause the disease conditions about to be described.

It may be well here to preface the discussion of the diseases produced by the two species of Gymnosporangia by referring to a case described by Ward¹⁵ which is apropos. The larch disease is due to the ravages of a fungus, *Dasysephypha Willkommii*, the hyphæ of which obtain access by wounds to the sieve tubes and the cambium of the stem, finally producing a cankerous malformation. The larch fungus is to be found on trees in their alpine home, but there it does very little damage and never becomes epidemic except in sheltered regions near lakes and in other damp situations. "How then are we to explain the extensive ravages of the Larch disease over the whole of Europe during the latter half of this century?" Ward asks. "In its mountain home the Larch loses its leaves in September and remains quiescent through the intensely cold winter until May. Then come the short spring and rapid passage to summer, and the Larch buds open with remarkable celerity when they do begin—i.e., when the roots are thoroughly awakened to activity. Hence the tender period of young foliage is reduced to a minimum, and any agencies which can only injure the young leaves and the shoots in the tender stage must do their work in a few days, or the opportunity is gone and the tree passes forthwith into its summer state. In the plains, on the contrary, the Larch begins to open at varying dates from March to May, and during the tardy spring encounters all kinds of vicissitudes in the way of frosts and cold

¹⁵ WARD, *Diseases in Plants*, 1901, p. 152.

winds following on warm days which have started the root action — for we must bear in mind that the roots are more easily awakened after our warmer winters than is safe for the tree. It amounts to this, therefore, that in the plains the long-continued period of foliation allows insects, frost, winds, etc., some six weeks or two months in which to injure the slowly sprouting tender shoots, whereas in the mountain heights they have only a fortnight or so in which to do such damage.”

May we not have a parallel case in the retarding influence of the conditions which surround the white cedar in its boggy home, and which influence is reflected in the structure of the annual rings of wood already alluded to and the development of the disease about to be described?

ADDITIONAL FACTS CONCERNING THE NORMAL STRUCTURE OF WHITE CEDAR STEMS.

Before beginning the pathological description, it may be well to say a few more words concerning the normal structure of the stem. The woody tracheids are elongated and marked with bordered pits in their radial walls. The bordered pits are large and well defined, both in the radial longitudinal section and in the transverse section. Resin canals (fig. 11) are entirely absent from the wood, and in this the general resemblance of the xylem of the white cedar to that of the pine ceases. The absence of a well-defined pith in *Cupressus thyoides* is also noteworthy. The phloem or bast region of a twenty-one-year-old stem consists of alternate concentric rings of hard and soft bast. The hard bast consists of bast fibres with thick chromophobic¹⁶ walls and obsolete lumen. The bast fibres are arranged in a single layer of cells in each of the annual rings of bast elements. Alternating with these are the soft bast layers, the layer latest formed being found next to the wood cambium. Numerous large circular and elliptical resin canals are found in the phloem region, breaking the continuity of the rings of hard and soft bast (fig. 11).

A stem forty-one years old shows essentially the same structure with some differences in the cortical region. The same uniformity in the size of all the tracheids is noticeable, there being no sharp

¹⁶A term proposed by Montgomery to describe the walls and protoplasm of cells that are refractory to stains.

delimitation of the annual rings of wood. An enumeration of the tracheids in a single row from pith to cortex is here given, as an expression of the relative size of each annual ring. The wood of the stem from which the enumeration is made is one inch diameter.

TABLE II.

| Number of Annual Ring. | Year. | Number of Tracheids. | Number of Tracheids in Autumn Wood. |
|---------------------------|-------|-------------------------|--|
| 41 | 1900 | 6 | 2 |
| 40 | 1899 | 9 | 2 |
| 39 | 1898 | 10 | 3 |
| 38 | 1897 | 14 | 2 |
| 37 | 1896 | 9 | 3 |
| 36 | 1895 | 6 | 2 |
| 35 | 1894 | 8 | 2 |
| 34 | 1893 | 8 | 2 |
| 33 | 1892 | 9 | 3 |
| 32 | 1891 | 9 | 3 |
| 31 | 1890 | 11 | 3 |
| 30 | 1889 | 13 | 3 |
| 29 | 1888 | 11 | 4 |
| 28 | 1887 | 13 | 3 |
| 27 | 1886 | 18 | 3 |
| 26 | 1885 | 15 | 3 |
| 25 | 1884 | 22 | 4 |
| 24 | 1883 | 18 | 5 |
| 23 | 1882 | 10 | 3 |
| 22 | 1881 | 10 | 3 |
| 21 | 1880 | 7 | 2 |
| 20 | 1879 | 15 | 3 |
| 19 | 1878 | 18 | 4 |
| 18 | 1877 | 14 | 3 |
| 17 | 1876 | 16 | 3 |
| 16 | 1875 | 19 | 3 |
| 15 | 1874 | 16 | 3 |
| 14 | 1873 | 17 | 3 |
| 13 | 1872 | 10 | 3 |
| 12 | 1871 | 13 | 2 |
| 11 | 1870 | 11 | 3 |
| 10 | 1869 | 11 | 2 |
| 9 | 1868 | 16 | 3 |
| 8 | 1867 | 16 | 3 |
| 7 | 1866 | 11 | 2 |
| 6 | 1865 | 21 | 4 |
| 5 | 1864 | 27 | 4 |
| 4 | 1863 | 22 | 3 |
| 3 | 1862 | 47 | 4 |
| 2 | 1861 | 22 | 5 |
| 1 | 1860 | 18 | 4 |

The tracheids of the first three years of growth are more rounded

in contour and their walls are thicker than those of subsequent years.

The phloem of a forty-one-year-old stem differs materially from that of a twenty-one-year-old stem in the absence of strongly marked layers of bast fibres. Bast fibres are present, but they are not in continuous layers. Even with the high power, it is difficult to trace their continuity. The resin canals occupy a definite area, viz., midway in the phloem. The medullary rays of the phloem are continuous with those of the xylem, running out to the active cork cambium (fig. 12). True cortical parenchyma is entirely absent from such stems. The cork is in several well-marked zones or bands. These bands are separated from each other by the several layers of cork cambium. Seven well-marked layers of cork cambium are met with in this forty-one-year-old stem. The outer one is about to be pushed off by the sixth layer of cork. The innermost cork cambium lies against the outer rows of phloem cells. Several old functionless resin canals are included in the mass of dead exfoliating bark. They are conspicuous as rounded or elliptical holes in the mass of cork cells. The external appearance of the bark of large trees is smooth than otherwise. It is usually from three-quarters of an inch to nearly an inch in thickness, light reddish-brown, and divided irregularly into narrow, flat connected ridges, which are often spirally twisted around the stem, and separated into elongated loose or closely appressed plate-like fibrous scales.

PATHOLOGICAL CONSIDERATIONS.

The pathological conditions which are followed by the striking increase in the size of the stems are of long duration, as evidenced by a microscopic examination of the swellings. The fight for supremacy, if such it may be called, is a long-drawn-out one. A section was made across the smallest stem canker which completely girdled the whole stem. It was found upon examining the abnormality that the same annual ring is not of a uniform thickness throughout, being thinner in some parts than in others. The rings are clearly much thicker than those of the normal stem. Sixteen rings in all were counted in the region of the canker. This increased width of the rings is due to an increase in the number of tracheids produced by the cambium. These tracheids, as well as

the cells of the medullary rays, are usually of a greater diameter than the normal, which also accounts for the greater width of the rings formed at the canker. These observations agree with those of Anderson¹⁷ upon the canker growth produced by *Dasyscypha resinarum*. The medullary rays of the swollen areas of the stem seem to increase somewhat in diameter. This increase of diameter is not due to the increase in the number of parallel rows of cells, but is due to the increase in diameter of the single row of parenchyma cells which is met with in the normal cross-section. These cells stain more deeply than the normal cells because of the granular contents. Further reference to this change of content in the medullary ray cells of diseased sections of the stem will be made with a description of the longitudinal section of the diseased regions.

If a number of tracheids in the annual rings of the swollen area of the sixteen years of growth be compared with the table displaying the number of tracheids in the annual rings of twenty-one years' growth, a wide difference is at once observable. The number of tracheids in the abnormal growth is clearly greater than in the normal one.

TABLE III.

| Number of Annual Ring. | Year. | Number of Tracheids. | Number of Tracheids in Autumn Wood. |
|---------------------------|-------|-------------------------|--|
| 16 | 1900 | 31 | 4 |
| 15 | 1899 | 24 | 6 |
| 14 | 1898 | 49 | 4 |
| 13 | 1897 | 54 | 5 |
| 12 | 1896 | 39 | 5 |
| 11 | 1895 | 50 | 7 |
| 10 | 1894 | 40 | 5 |
| 9 | 1893 | 29 | 4 |
| 8 | 1892 | 42 | 5 |
| 7 | 1891 | 25 | 4 |
| 6 | 1890 | 26 | 7 |
| 5 | 1889 | 21 | 4 |
| 4 | 1888 | 20 | 4 |
| 3 | 1887 | 12 | 2 |
| 2 | 1886 | 10 | 3 |
| 1 | 1885 | 10+px. | 3 |

¹⁷ ANDERSON, ALEXANDER P., *Dasyscypha resinaria* causing canker growth on *Abies balsamea* in Minnesota, *Bulletin of the Torrey Botanical Club*, XXIX, pp. 23-34.

One of the most frequent results of the action of fungi is that of a stimulus given to cell division. Mention in this connection must be made of the swellings on the stems of silver firs, whose cortical tissues are infested by *Æcidium elatinum*; the increased growth of the cowberry through the attack of *Melampuspora* (*Calypsotheca*) *Gæppertiana*;¹⁸ of the larch through the influence of *Peziza* (*Helotium*) *Willkon.mii*.¹⁹ Still more frequently the infested parts are stimulated to display abnormal growths. Flowers and fruits of various species of plants are transformed in a most peculiar manner by fungi belonging to the genus *Exoascus*. The disease of the silver fir, however, caused by *Æcidium* (*Peridermium*) *elatinum* is the most appropriate one to compare with the canker knobs produced on the white cedar by *Gymnosporangium bisepitatum*. The mycelium of this fungus, according to Hartig, is perennial in the cortical and bast tissues of the stem, and even penetrates the cambium and the wood. With the spread of the mycelium, the swellings or canker spots increase in size, and if present on the stem of a vigorous tree, they may attain to large dimensions. At such places the tissues of the cortex and bast become fissured and dry up here and there, as far as the wood, giving the whole exterior of the swelling a rough, shaggy appearance. The swellings resemble much in external character those described by the writer as occurring on the white cedar in New Jersey. Anderson²⁰ describes the changes produced in the cortex of *Abies balsamea* by *Dasyscypha resinaria* in the following quotation from his paper: "In the bark of the canker, the periderm as well as the primary cortex, and outer layers of the secondary cortex, are very soon cut off by the formation of a new phellogen layer. This causes the death of the cut-off layers of the bark, which dry up sooner than in the normal. The resin canals are also cut off and disturbed, and their resin contents begin to diffuse into the surrounding tissues, but mostly collect in the resin vesicles or 'blisters,' which are also formed sooner in the primary cortex of the canker than in the normal bark. The resin of the canker vesicles is forced out by the increased pressure on the vesicle, by the shrinkage of the surrounding dead layers of the bark, cut off by

¹⁸ HARTIG, *Text-Book of the Diseases of Trees*, 1894, p. 161.

¹⁹ HARTIG, *loc. cit.*, p. 120.

²⁰ ANDERSON, *loc. cit.*, p. 29.

the new phellogen. The resin thus forced out runs down the trunk of the tree, the more volatile substances evaporating, leaving the solid resin, which hardens and gives the trunk a glazed appearance easily seen at some distance from the tree." *Peziza* (*Dasyscypha*) *Willkommii* and *Æcidium* (*Peridermium*) *elatinum* cause similarly an increased growth of the cortex. In summer the growth of the mycelium of the former ceases and an unusually broad layer of cork is formed, for the protection of the tree, along the boundary between the sound and diseased tissues. Year by year the canker spot enlarges and the conflict between parasite and host plant may remain long undecided. Hartig found in the Tyrol larches still alive with blisters of a hundred years' standing. The second fungus, whose mycelium stimulates growth in a very marked manner, is perennial in the cortical and bast tissues of the stem, and even penetrates the cambium and the wood. The influence of the fungus is to induce the increased formation of the wood, but especially the more vigorous development of the cortex.

This account with reference to the increased activity of the phellogen (cork cambium), due to the fungi mentioned, describes in a fairly accurate manner the method of augmented growth in the white cedar caused by *Gymnosporangium biseptatum*. Four successive cork cambial layers have been developed in this sixteen-year-old stem, with the possibility of more that have been exfoliated. The newest phellogen has developed inside the phloem, cutting off from the more internal layers three concentric layers of hard bast. Not only has the hard bast been cut off from the inside of the stem, but also the resin canals, with, however, only a slight exudation of resin, the corky flakes remaining almost quite dry. The three outer cork cambia have only affected the primary cortex, and between these layers of phellogen the resin canals have expanded to their widest diameter. The layers of cork cambium take a somewhat sinuous course in running around the stem, so that they apparently loop in and out among the rapidly dying cells.

The hyphæ of the fungus live apparently in the cells of the wood cambium and those of the phloem recently cut off from the cambium. This is evidenced by a study of the cells. The hyphæ in cross-section occupy the lumen of the cells, for, in addition to the cellulose cell wall of the host, there are rounded or elliptical rings filled with granular matter (figs. 18, 19). These rings are the

transversely or obliquely cut hyphæ which, by their presence, stimulate the cambium to increased activity. With the exception of these there seems to be no other attributable cause for the formation of the swellings, because the wood at this stage of the disease is free from all appearance of disintegration. It is, however, otherwise when the disease has progressed for some years. One remarks this on studying the sections of a canker that has progressed in development for some ten or more years. In all of the larger swellings studied by the writer, the cambium had been killed in a number of places. The dead spots vary in size in different cankers, but they seldom become confluent by extending completely around the stem or branch. When they meet so as to girdle the stem, the stem dies. More often the dead area is small, remaining about the same size for a number of years. The living cambium makes an effort to repair the damage, but this it is not able completely to do on account of the presence of the mycelium in the tissues. A cavity or pocket finally results at the dead spot with the increase in number of the annual rings (fig. 14). As with the disease of *Abies balsamea* described by Anderson, often several such cavities are formed when the cambium has been killed at more than one spot, and these cavities or pockets contain hardened resin. In the white cedar a comparatively small amount of resin collects, but in *Abies balsamea* the amount is quite considerable. In stems of white cedar that have been long diseased and that are dead above the swelling the brown bark cracks off, exposing the wood, the external surface of which is ventricose (fig. 14). The sap-wood of such badly diseased swellings has become porous, partly rotten and divided up into plates by the pores, the cracks or the fissures that abound. The heart-wood is still firm. Under the microscope this breaking down of the sap-wood does not seem to follow an absorption of the middle lamella of the cell wall by ferment action, but is due to a springing free of the lignified portion of the cell wall. Later the walls seem to break across and pieces of lignified cell wall, some U-shaped, some Y-shaped, hang free along the edges of the fissures thus formed. Here the disease has progressed to its fullest extent (fig. 32).

The hyphæ from the point of infection grow through the cortex and then spread vertically up and down through the phloem. By the second year they have established themselves in the cambium

and in its immediate neighborhood (fig. 18). The pathological conditions set up by these hyphæ have been described, but in addition to the increase of the bast and the wood, we have an increase in the number of cells in the cortex and the bark. The course of the hyphæ and their distribution throughout the swellings will be described more in detail. A brief mention at this point suffices to draw attention to them.

THE PLUGGED TRACHEIDS.

The wood of the abnormal regions of the stem shows in addition to the hyphæ brown-colored spots which are absent in stems of normal proportions. Without discussing at this juncture the nature and significance of these brown spots, which are due to the plugging of the tracheids, it is appropriate to discuss the distribution of the spots throughout the diseased regions of the stems. Plugged tracheids are found in the swellings with sixteen rings of growth, beginning with the fourth annual ring of wood. Here they are seen in the spring wood. Counting the number of such plugged tracheids in a half-circle of the fourth annual ring of wood and in the rings of successive years of the same stem, we obtain the following numerical statement:

TABLE IV.

| Seasonal Wood. | Year. | Number of Plugged Tracheids. |
|--------------------|-------|------------------------------------|
| Summer. | 1 | |
| | 2 | 18 |
| | 3 | 23 |
| Spring. | 4 | 22 |
| Spring and Summer. | 5 | 32 |
| Autumn. | 6 | 18 |
| Summer. | 7 | 12 |
| Spring and Summer. | 8 | 11 |
| Summer and Autumn | 9 | 16 |
| End of Spring. | 10 | |
| | 11 | |
| | 12 | 10 |
| | 13 | |
| | 14 | |
| | 15 | |
| | 16 | |

An inspection of the table shows that in small swellings the

plugged tracheids are confined almost entirely to the summer wood, and occur in largest number in the first six or eight years of growth. Very few are found in the annual rings subsequent to the ninth.

Older stem cankers show these plugged tracheids more plentifully from the first annual ring of wood laid down to the last one (figs. 16, 17). The larger excrescences have them in greatest number. The smaller excrescences are without them. At the point, however, where the tissues of the swellings join the main portion of the stem, these plugged tracheids are so numerous that they form well-marked concentric bands. The following statement roughly expresses the position and abundance of the plugged tracheids in the several annual rings of a swelling with well-marked excrescences.

Second Year Wood. Summer. Abundant, forming a compact circular zone.

Third Year Wood. Spring. Abundant, forming a loose zone.

Fourth Year Wood. Summer. Sparse, except one area where the plugged tracheids are closely aggregated together. At this point the ring is much narrower, taking a U-shaped bend inward. The autumn wood here is wanting. The fourth annual ring is, therefore, continuous except at this one point, where it becomes bent inward. Instead of the fifth year wood following this indented portion of the fourth year wood, it fills up the indented area with additional tracheids, so that at the end of the fifth year the course of the autumn wood again conforms to a circular outline.

Fifth Year Wood. Autumn. Sparse.

Sixth Year Wood. Late summer. Plentiful.

Seventh Year Wood. Summer. Autumn. A few plugged tracheids are found in the summer wood. More are met with in the autumn wood.

Eighth Year Wood. Late spring. The plugged tracheids are very abundant and in a definite circular zone.—Summer. Abundant in two circular zones. Late summer. Scattered.

Ninth Year Wood. Summer. Very few, but the plugged tracheids apparently become brown lines coterminous with the medullary rays.

Tenth Year Wood. Autumn. Abundant and occupying in a circular zone the region of the autumn wood. The same brown lines are traceable running out to the cortex.

Eleventh Year Wood. Late summer. Plentiful in a definite zone. A few in the autumn wood.

Twelfth Year Wood. Spring. In a definite zonal band, two or three tracheids deep. A few in the summer wood. A ring of scattered tracheids at the beginning of the autumn wood.

Thirteenth Year Wood. Whole year. Here the small excrescence began its growth. It is limited on both sides by dead tissue. The plugged tracheids form several circular zones both in the spring and summer woods. Three well-marked circular zones of plugged tracheids are clearly distinguishable, forming with their aggregation an almost continuous area involving most of the tracheids of the spring and early summer woods. Beyond the area with the largest number of these plugged tracheids occurs the small excrescence which has grown over the adjacent bark at the dead areas, producing a characteristic fissure. The disposition of these plugged elements in concentric rings in the several annual cylinders of wood is somewhat analogous to the disposition of the resin canals in *Abies balsamea*, diseased by *Dasyscypha resinaria*, as described by Anderson. This botanist finds that these are arranged in circular rows and in all cases follow the development of the above-mentioned fungus. According to the same author, Nottberg produced these resin canals experimentally in the wood and branches of *Abies pectinata* by fracturing the branches. The characteristic canal chains were formed in the wood near the fracture three months after the wound had been made.²¹

The phloem and cortex regions of the swollen areas are remarkable for the increase in the number of elements. The cork, hard and soft bast, representing the previous activity of the cambial layers, are pushed off more rapidly than in a normal undiseased area (figs. 13, 14). New layers of hard and soft bast are formed constantly by the wood cambium, and the noteworthy features of such phloem is that the bast fibres do not form so continuous a circle of growth, but are isolated in patches. The cells of the soft bast are more irregular in outline (fig. 13). The resin canals in such cross-sections are also more inconstant in outline. Some of them are large and of irregular shape; others are circular and small. The resin canals in the normal state are, as a rule (not always), elliptical in cross-section. Where the cortex of the excrescence

²¹ ANDERSON, *loc. cit.*, p. 31.

meets that of the unmodified stem it is much reduced in width, and there are no cortical cells where, by the folding over of the swelling, forceful compression occurs. The bast fibres in transverse section are, as a rule, rectangular with rounded corners. The lumen has almost completely disappeared. In unstained mounts these elements have the luster of German silver. These fibres are more continuous in some places than in others. Their continuity is only broken by the cortical medullary rays.

Longitudinal sections of two swellings were studied. The swellings used to make the sections may be described as follows: The first one forms a burl-like outgrowth on one of the smaller lateral branches which had grown through the activity of the fungus very considerably in size, the end being rounded and clubbed. The other swelling represents a malformation of the main stem and a branch, a section of which is in general Y-shaped. The thicker part of the swelling represents the stem of the Y. These sections were stained with methyl-green. The normal tracheids are chromophobic. The bordered pits are well marked in all of the tracheids.

The plugged tracheids mentioned in the consideration of the transverse sections are well marked. They stain in general of a dark-green color, and the lumen seems to be enlarged and filled with granular contents. The ends of such tracheids are more rounded than the ends of normal ones. The cell-lumen is larger. The wall is more wavy and the course of the elements more irregular. In some of these plugged tracheids the contents seem to be more or less granular. These become dark-green in color by the use of the methyl-green. That these longitudinally directed plugged tracheids correspond to the brown spot referred to in the description of the several cross-sections is easily demonstrated by observing their course in the sections of lateral branches found in the longitudinal sections of the swellings. It is observable that the longitudinally directed tracheids filled with granular matter take a sharp bend and run into the branch, where they are seen in transverse section. The medullary ray cells also of such sections become deeply stained when methyl-green is applied. Tangential sections of the swellings show the medullary ray cells stretching across the tracheids in a gridiron fashion. The parenchyma cells of the medullary rays are long compared to their diameter. The ratio of 5 to 1 will express in an approximate manner the relative length and diameter of such parenchyma cells.

CONTENTS OF PLUGGED TRACHEIDS AND FILLED MEDULLARY RAY CELLS.

The Unverdorben-Franchimont reaction with copper acetate was used as a special reagent to determine the presence or absence of resins and terpenes.²² It was thought that the material plugging the tracheids and filling some of the medullary ray cells might be of a resinous nature. The reaction is indecisive as to the material in the tracheids. An emerald-green color is produced by the copper acetate in the area of wood most affected by the fungus and where the active formation of the wood and bast took place. This green color is confined to the newly formed sap-wood and to the immediate neighborhood of the most active mycelial growth. The appearance of the emerald-green color indicates the presence of resin, and, in fact, in thin longitudinal sections of the wood of the stem at the swelling there is found a granular matter which stains a malachite-green. This material, which reacts to the copper acetate, occurs as a peripheral layer about the brownish matrix in the center of the filled medullary ray cells and the plugged tracheids, and this is most pronounced where the influence of the fungous parasite seems to be most marked. In some cases the green color indicates that whole medullary ray cells contain a resinous material. The contents of the resin canal cells of the phloem and of the cortex react to the copper acetate, and the dried resin which occurs on the surface of and in the fissures of the bark becomes of a striking malachite-green color. These latter reactions confirm the Unverdorben-Franchimont test. The green color imparted to the wood is confined to patches and is not generally distributed. The brown material in general of the plugged tracheids and medullary ray cells is not influenced by the copper acetate. That this reaction seems to indicate the presence of resin in the most diseased areas and another fundamentally different substance is indicated by the fact that adjoining cells will have their contents colored emerald-green, while others will remain uniformly uncolored. In a transverse section of the area of wood stained green, the contents of the plugged tracheids (figs. 16, 17) still retain their brownish-yellow color. Notwithstanding these facts, one point seems to be definitely settled, viz., that the presence of the mycelium in the

²² ZIMMERMANN-HUMPHREY, *Botanical Microtechnique*, pp. 90, 91.

sap-wood and cambium leads to the accumulation of resin, a brownish-yellow material which appears to be fungus gamboge, as indicated by the following test: A solution of ferric-chloride colors fungus gamboge olive-green or blackish-brown, and in the sections of white cedar so treated a decidedly blackish-brown color is obtained. The material in the tracheids is, therefore, named tentatively fungus gamboge. Besides this material, which seems to form the matrix, there are numerous small rounded grains which plentifully fill the medullary ray cells. These granules stain brown when iodine solution is used, green when methyl-green is used, and brown when Bismarck-brown is applied. The substances which then collect in the diseased stems of white cedar through the metabolic changes stimulated by the fungus mycelium are tentatively the following: Proteid bodies, in small rounded granules; resin, which is confined to the areas of stem undergoing the most rapid histologic changes; fungus gamboge, which with the other materials referred to fills the medullary ray cells and plugs the tracheids. Besides these, there are amorphous masses of substance in some of the medullary ray cells. These in the natural state are yellowish in color. When the sections are stained with methyl-green, these masses become green in color. It is impossible to state at this time what these amorphous masses really are.

With strong iodine solution the walls of the tracheids color a deep brownish-yellow, and this reaction is marked in both the longitudinal and the transverse sections.

THE MYCELIUM OF *GYMNOSPORANGIUM BISEPTATUM*.

A study of the mycelium yields some interesting results. These results become of importance when a comparison of the mycelia of the different species of *Gymnosporangium* is made with reference to their growth and duration. Farlow²³ briefly sketches the character of the mycelium in the American species studied by him. "The mycelium does not differ much from that commonly found in the other Uredineæ. It is irregular, much branched and cross partitions are rather numerous. Unlike, however, the mycelium of some of the Pucciniæ, that of the species of the present genus is limited in extent, and is not found throughout the whole of the

²³ FARLOW, *The Gymnosporangia or Cedar Apples of the United States*, 1880, p. 10.

plant on which it is growing, but is confined to certain portions of the stems or leaves. The mycelium of most of the species is perennial—that is, the mycelium which has produced a crop of spores (figs. 29, 30) one year, will the next year, under ordinary circumstances, produce another crop in or near the same place.” The explanation of the difference in the character of the different abnormal growths produced by the various species ‘of Gymnosporangia is to be sought in the amount and extent of the mycelium, the rapidity of its growth and its duration. We have in a rapidly growing annual species, viz., *G. macropus*, a large, rather spongy excrescence, which shrivels in drying. The excrescence is more dense in the perennial species of slower growth, viz., *G. globosum*. The mycelium of *G. biseptatum*, according to Farlow, is comparatively limited in amount, and does not increase rapidly, and in consequence the formation of the annual wood layers is not prevented, nor the nutrition of the branches above much interfered with. The mycelium, as described by Farlow, is found principally in the region of the cambium, and acts rather as a stimulant than as a destructive agent. There is in *G. Ellisii* a more luxuriant and rapidly growing mycelium, which extends along the smaller branches and is abundant enough to interfere with the nutrition of the infected branches. The consequence is that the branches above become short and stubby, and at length densely fasciated. The branch below the fungus remains normal in character, so that instead of a nodose swelling we have a tuft of short branches borne on the end of a normal branch.²⁴

With this brief résumé of the character of the mycelium in the different species of *Gymnosporangium* living in the wood of coniferous trees, it is important to make a more detailed study of the character of the mycelium and its relation to the cells of the host in *Gymnosporangium biseptatum*. Very little of a definite character can be ascertained by a study of the transverse section of the diseased wood of the white cedar. Here and there the cut ends of the hyphæ are seen, and occasionally the knuckle-like portion of one that is bent is seen in the cross-section (figs. 18, 19). The hyphæ, which are instrumental in stimulating the production of additional wood and bast, live in the cells of the wood cambium. This is evidenced by a study of the cells. The hyphæ in cross-

²⁴ See *ante*.

section apparently occupy the lumen of the cells, for, in addition to the cellulose cell wall of the host, there are rounded or elliptical rings filled with granular matter. The difficulty of clearly tracing the hyphæ in a cross-section is almost entirely removed by careful study of longitudinal sections. Such longitudinal sections reveal the following distribution of the hyphæ and their relation to the cells of the host:

The hyphæ are of a brown color, and can easily be traced by means of the contrast which this color affords to the colorless tracheids and to the medullary ray cells which have stained a bright-green color with methyl-green. The mycelium is not abundant, and if we imagine the host cells to be macerated away, leaving the mycelium, it would form a reticulum of large open meshes much in appearance like a coarse fish-net, only not so regular (fig. 22). The hyphæ are variously curved, gnarled or knuckled (fig. 22). Their course is somewhat sinuous, or an undulate one, although in many cases the larger hyphal strands are perfectly straight. They occur in all parts of the wood of the swelling, and are associated in general with the plugged tracheids and the enlarged medullary rays, which contain the yellowish granular matter to which reference has already been made. The plugging of some of the tracheids in the several annual rings of wood with yellowish granular material and the enlargement and filling up of the medullary ray cells seems to be correlated with the presence of the mycelium. The tracheids and medullary ray cells distant from the strands of the mycelium are without these evidences of nutritive changes, followed by the filling of the cell cavity by the granular waste, or reserve (?) products. The hyphæ are marked by numerous transverse partition walls, and these are sufficient to indicate that the fungus belongs to the higher series of fungal types. Some of these hyphal cells are long and cylindrical. Others are shorter and more cheese-box-like in form.

RELATION OF HYPHÆ TO HOST CELLS.

The hyphæ grow into and through the medullary ray cells, and it is through these cells that the mycelium maintains its continuity from annual wood ring to annual wood ring. It is this growth through the medullary rays that accounts for the perennial habit of the fungus. At best the growth of the fungus is a slow one, as the

hyphæ are nowhere abundant, and where they do occur they seem to grow with the tracheids. The evidence of intracellular growth is clear.²⁵ In one set of medullary ray cells a hypha is found which forms an enlargement against a transverse partition wall before penetrating it by secretion of a ferment (fig. 22). Fortunately for clearness of observation, the end walls of two adjoining cells are slightly separated, leaving a lens-like intercellular space (fig. 23). Through this space the hypha, contracted to a narrow thread-like bridge, is seen to pass, enlarging again on the other side (fig. 23). The hypha which thus penetrates the cell wall passes to the other end of the same medullary cell, where it enlarges into a knob like extremity (fig. 23). It, however, gives rise to a branch in the middle of the medullary ray cell. This branch grows out transversely by means of a bordered pit into the lumen of a wood tracheid, through which it runs to the next medullary ray lying parallel to the first. Here a new branch is found at right angles to its former course through the tracheid, which enters a medullary ray cell. This branch in turn produces another one at right angles to itself, and this again another one which runs into new medullary ray cells. The description of the course of this hypha, which is clearly traceable in the longitudinal section of the swollen stem, epitomizes the course of practically all of the hyphæ studied in the several longitudinal sections. The hyphæ enter the longitudinally directed wood tracheids through the path of least resistance, viz., through the membrane of the bordered pit (figs. 24, 24a, 25, 26). In several instances this mode of exit and entrance is clearly traceable in the sections. By following the course of a hypha through the lumen of a tracheid it is found suddenly to dip down at the pointed extremity of the tracheid, opposite to the last bordered pit, and after disappearing from focus it again appears in another tracheid. By carefully focusing it is demonstrated that the hypha passes through the bordered pit, and after taking a U-shaped bend it appears again on the original level in another tracheid (fig. 22).

The mycelium does not show any relationship to the nuclei of the host cells, such as has been demonstrated to be the case with the

²⁵ Farlow found in *G. macropus* the mycelium in the leaves where there are haustoria [*sic*] which enter the parenchymatous cells. The fact that the mycelium grows in the leaves and not in the stem may account for this difference in growth.

hyphæ of endotropic mycorrhiza. Groom²⁶ and Magnus²⁷ have both worked upon this problem, and both botanists have shown that in the case of the hyphæ of mycorrhiza fungi they enter a cell because they are attracted thither by a chemotropically active substance and grow toward the nucleus, because that substance is present there in optimum proportions. These investigators conclude that the chemotropically active substance attracts the hyphæ and is manufactured in the cell infected, and particularly in the vicinity of the nucleus of that cell. No clearly defined relationship of this kind is discoverable in the medullary ray cells of the white cedar. The hyphæ run straight through many of the cells without deviating from their course.

This distribution of the mycelium in *G. bisepatum* seems to be similar to the distribution of hyphæ in *G. Ellisii*, as described by Farlow. The mycelium of this species, according to Farlow, is of rather large size and in cross-sections of the stem is seen to follow the medullary rays, sometimes extending nearly to the center of the stem, and occasionally forming partial circles between the annual rings. The greater part of the mycelium in *G. Ellisii*, according to Farlow, is found near the cambium, it collects in masses in the bark to form the sporiferous bodies which originate at some little distance beneath the surface.

MYCELIUM OF GYMNOSPORANGIUM ELLISII.

The mycelium of *Gymnosporangium Ellisii* is more copious than that of *G. bisepatum*, and its activity seems to be more marked in producing pathological changes in the tissues of the host. It may be traced in both radial and tangential longitudinal sections to the best advantage. The development of the hyphæ of the mycelium in the sections studied by the writer is in a longitudinal rather than in a transverse direction (fig. 24). The main hyphæ of the mycelium are longitudinal ones, and these anastomose with each other by the formation of short hyphæ developed at right angles to the longitudinal ones. The course of the main hyphæ is approximately a straight one, although of necessity there is some

²⁶ GROOM, On *Thismia Aseræ* (Beccari) and its Mycorrhiza, *Annals of Botany*, IX, pp. 327-360.

²⁷ MAGNUS, WERNER, Studien an der endotropischen Mycorrhiza von *Neottia nidus-avis* L., *Jahrbücher für wissenschaftliche Bot.*, 1900, p. 205.

bending from a straight line as they run from tracheid to tracheid (fig. 25). Some annual rings are noted for the considerable number of hyphæ present. Others are marked by the small number and weak development of the hyphæ. The color of the hyphæ is an umber-brown, practically the same as that of the hyphæ of *Gymnosporangium biseptatum*. Occasionally hyphæ in *G. Ellisii* are found that are yellowish-brown in color. The hyphal strands are characterized by the well-marked transverse partitions, which are evident even under the low power of the microscope. It may be remarked here that the general course of the mycelium can be clearly followed by the low power alone. The mycelium is more abundant in the cortex and comparatively less abundant in the xylem. Some peculiarities of structure of the hyphæ of this species easily differentiate it from *G. biseptatum*. The hyphæ of *G. Ellisii* form, as revealed by the high power of the microscope, a somewhat irregular reticulum (fig. 24). These hyphæ are characterized by the presence of larger or smaller nodose or ventricose hyphal cells (figs. 25, 26, 27), which are found in considerable numbers in the length of each hyphal strand. These swollen or enlarged cells are found most frequently in the irregular intercellular spaces, filled with brownish material produced by the pathological changes induced in the host by the growth of the fungus. Occasionally these ventricose hyphal cells are found as lateral branches of the main longitudinally directed hyphæ. Their shape may be spherical, ellipsoidal, oblate-spheroidal, napiform or fusiform (figs. 25, 26, 27). They are of the same umber-brown color as the other unenlarged hyphal cells, and are most numerous in the cortical region and in the aforementioned pathological areas filled with brown material.

RELATION OF HYPHÆ OF *G. ELLISII* TO HOST CELLS.

The course of the hyphæ in the stem may be briefly described as follows: The straight hypha runs through the lumen of the tracheid until it comes to a bordered pit which lies in the direction of its growth (figs. 24, 24a). This bordered pit is entered, and by a solution of the middle lamella of the cell wall at this point it crosses to a neighboring tracheid, when it again takes a longitudinal direction. Sometimes two or three tracheids are crossed by the hypha before it again takes an up-and-down course (fig. 24).

The hypha, as it passes through the area of the bordered pit, enlarges to fill the space formed when the middle lamella of the cell wall at this point is dissolved by ferment action (fig. 24*a*). The hypha at this point, therefore, becomes in shape like a double convex lens. Again, a hypha that runs in general longitudinally in the tracheids may leave these and enter a medullary ray cell, where it courses transversely, enlarging meanwhile in the medullary ray cell and giving off short rounded branches which may be called tentatively haustoria. A hypha that enters a tracheid in one direction may form two branches, one a short, lateral, downward-directed branch that ends in one of the large ventricose cells (fig. 27) to which reference has been made, and another branch which runs to the end of the tracheid and leaves it through a bordered pit to enter another tracheid. Another hypha runs lengthwise until it comes opposite to the pointed end of another tracheid, where a row of five bordered pits is seen in transverse section. For each of these bordered pits the longitudinal hypha gives off a branch (figs. 24, 24*a*). Each branch thus formed swells in the space of the bordered pit to form a lens like enlargement before the branch enters the contracted lumen at the pointed end of the other tracheid. All of these appearances are illustrated in the annexed figures (figs. 24, 24*a*, 25, 26, 27, 28).

The course of the hyphæ in the areas of stem that have been transformed pathologically into a broken-down mass of a brown color, forming pockets throughout the wood, is more irregular. Here the hyphæ forming the mycelium bend and twist about, now forming an enlarged ventricose hyphal cell, and again producing such a swollen cell as the termination of a short lateral branch. Short stubby branches are also formed in the course of these same hyphæ, consisting in most cases of a single short cell. The hyphæ of these brown areas have also increased considerably in diameter, being much thicker than those of the mycelium which grows in the tracheids. The larger hyphæ are found in the cleft-like intercellular spaces and grow in and out between the dead and broken-down cells, as well as through the resin-like substance which fills the pockets to which reference has been made above.

The hyphæ in the smaller transverse sections of the diseased stem are also clearly traceable. They are seen as purplish-brown rings in the lumen of the tracheids (figs. 20, 21). Several adjacent

tracheids will have hyphæ coursing through them, and occasionally two or three hyphæ are met with in a single tracheidal cavity. Where these hyphæ, by branching, cross transversely other tracheids, they are observed in cross-sections of stem as short threads, or as U-shaped or V-shaped elements of a purplish-brown color. Whenever these hyphæ in their branching enter one of the brown areas with cleft-like cavities, they grow through the brown mass, enlarging meanwhile in diameter, and grow out into the cleft, where they branch and rebranch in an irregular manner, swelling here and there into the nodose or ventricose cells referred to above (fig. 27). Occasionally the hyphæ are found growing outward through the medullary ray cells, but this seems to be the exception rather than the rule. This fact affords another of the characters of the mycelium of *G. Ellisii* which differentiates it from that of *G. bisepatum*, also found on the white cedar.

The distribution of the tracheids containing the hyphæ, disposed as above described, is for a transverse section of stem seven years of age, as given in the accompanying table. The number of tracheids in which hyphæ are found is estimated for one-half of each annual ring. The widest annual ring is that of the third year, and this increased width is closely correlated with the diseased condition of the stem for that year:

TABLE V.

| Number of Annual Ring. | Year. | Number of Tracheids. | Number of Tracheids in Autumn Wood. | Number of Tracheids with Hyphæ $\frac{1}{2}$ Annual Ring. |
|------------------------|-------|----------------------|-------------------------------------|---|
| 1 | 1894 | 22 | 2 | 13 |
| 2 | 1895 | 16 | 3 | 6 |
| 3 | 1896 | 30 | 4 | 26 |
| 4 | 1897 | 10 | 3 | 17 |
| 5 | 1898 | 9 | 2 | 34 |
| 6 | 1899 | 5 | 1 | 21 |
| 7 | 1900 | 5 (?) | | 12 (?) |

The brown areas are by far the largest and almost confluent in the third annual ring of wood, and therefore only four continuous radial strips of healthy xylem are to be found in the growth of the third year. The enumeration for the seventh year is incomplete,

because the stem was dead along the radius of stem chosen for the computation of the tracheids.

The mycelium in the cortex is well marked. The hyphæ grow both into and through the cortical cells, and are found in the larger and smaller intercellular spaces. Their direction of growth is less definite than in the wood, and they, therefore, form a complex of twisted and curved hyphæ which run apparently through the medio-cortex in an indefinite manner. The rounded enlargements of the hyphal cells above mentioned are also found.

PATHOLOGICAL CONDITIONS OF STEM INDUCED BY THE MYCELIUM OF *G. ELLISII*.

The pathological condition of the stem of white cedar induced by the parasite are very different from those produced by the mycelium of *G. bisepatum*. It may be stated at the outset that the diseased conditions are much more severe when the mycelium of *G. Ellisii* is the pathological agent, although the swellings never become so large and globose as those formed by the stimulating influence of the mycelium of *G. bisepatum*. The witches' broom-like character of the malformations caused by *G. Ellisii* have already been described (figs. 6, 8). Observations in the field, after part of this paper had been written, reveal some characteristic features of the disease not mentioned then. The disease, except in young trees, seems if it attacks older trees, to be confined to the short lateral branches of the trees, as they form a pure growth in the cedar swamps of New Jersey. Sometimes all of the larger branches from the lower part of a tree to the top will be fasciated. The branches live for a long time before death finally ensues, and they consequently have a gnarled and knotted appearance which gives to a large tree badly diseased an unsightly appearance. Birds, such as the fish crow, take advantage of the flattened, closely crowded condition of the branchlets to build their nests under cover of the dense and crowded mass of leaves which forms a closely set crown of foliage (fig. 6). The photographs of diseased lateral branches (figs. 6, 8), one of which supports a nest of the fish crow, show the general appearance of the disease when it has progressed to the point of involving the whole branch.

In the seven-year-old stem above described the wood is badly broken down, and in place of the healthy tracheids there are irregu-

lar wedge-shaped masses of a rich brown color, consisting of the broken-down cells, a mass of hyphæ and a yellowish-brown matrix formed as a waste product by the host cells that are attacked by the fungal parasite. These masses of dead tissue proceed radiately outward. Their inner side is more or less evenly rounded and conforms to the general concentric arrangement of the annual rings (fig. 31). Their outer edge is more or less irregular, as the disease progresses by proceeding outward along the wedges of wood between the medullary rays (fig. 31). These diseased areas may become more or less confluent as the pathological tissue increases in amount by the spread of the fungus antagonistic to the host (fig. 31). Where these wedge-shaped brown areas touch the cortex the cortical cells become involved, assuming a darker, richer brown color with the death of the cells attacked. As these brown patches increase in size, the hyphæ which have grown out into them keep pace with the dissolution of the healthy tissues, until, as before mentioned, they form a complex of considerable extent.

The breaking down of the tracheids begins much in the same manner as in the disease of the white cedar induced by *G. bisep-tatum*, but the final result is different. The same springing loose of a part of the lignified cell wall is observable (fig. 32). When two adjacent tracheids have been thus affected, the middle lamella is dissolved away and a cavity, two tracheids in diameter, is formed. If three or four adjoining tracheids are involved, the space becomes larger (fig. 33). These spaces are filled with a brown residual material, and by the confluence of a number of smaller brown diseased areas the wedged-shaped diseased spots are formed, which later become fissured by the appearance of crack-like intercellular spaces. In older stems, the appearance of the diseased brown areas and the increase in width of the annual wood-rings seem to be correlated. The fifth and sixth annual rings in a stem eleven years old seem to be most involved, and here, with the exception of one small unaffected patch of tissue, the brown tissue forms a continuous band of variable thickness and pathological appearance about the stem. The spring wood of the sixth year here seems to be most involved. From this ring arms of diseased wood radiate out through the seventh, eighth, ninth, and on one side of the stem to the cortex through the eleventh and last annual ring of wood. An enumeration of the number of tracheids in a radial row

from the fifth outward is presented in tabular form, as showing the variation and increase in size of the several annual rings of wood in the abnormally developed tissues of the stem. The variation in the size, shape and color of the tracheids is a peculiarity of the twelve-year-old stem studied. These variations are most marked in the fourth and the eighth annual rings. The tracheids of the fourth annual ring of wood are thicker than the normal, and of a decided yellow color. Those of the eighth annual ring are decidedly variable in shape. Some of the tracheids are circular in cross section, others are elliptical, while others are rectangular and more or less irregular. This departure from the normal structure of the tracheids is directly traceable, the writer believes, to the stimulation produced by the presence of the fungus in the tissues of the host plant.

TABLE VI.

| Number of Annual Ring. | Year. | Number of Tracheids. | Number of Tracheids in Autumn Wood. |
|------------------------|-------|----------------------|-------------------------------------|
| 1 | 1889 | 7+px. | 2 |
| 2 | 1890 | 7 | 1 |
| 3 | 1891 | 9 | 2 |
| 4 | 1892 | 29 | 3 |
| 5 | 1893 | 21 | 3 |
| 6 | 1894 | 23 | 5 |
| 7 | 1895 | 27 | 4 |
| 8 | 1896 | 32 | 5 |
| 9 | 1897 | 28 | 5 |
| 10 | 1898 | 33 | 5 |
| 11 | 1899 | 16 | 3 |
| 12 | 1900 | 22 | 3 |

A comparison, however, of the width of the several annual rings of older and younger stems shows that the increase in the number of tracheids is marked, especially in the immediate neighborhood of the hyphæ. There is, however, not that marked increase which is noted for the stems abnormally swollen by the action of the mycelium of *Gymnosporangium bisepatum*. The same brown patches of pathological tissue are seen in branches an inch and a quarter in diameter. Here, if the disease is confined more especially to the smaller branches, the brown areas are more rounded and appear as isolated brown specks when a cross-section is made. The smaller

branches, if early infected, are more badly diseased, as evidenced by the larger size and confluent condition of the dead tissues, than the heavier branches, if infection takes place after the branch has reached considerable size. The writer has no evidence that the disease spreads down into the wood of the older portion of the branch from the smaller branches by the longitudinal growth of the hyphæ, although it is within the range of probability that this downward growth does take place.

CONCLUDING REMARKS.

That the metabolic activities of the cells invaded by the mycelia of the two parasites above described are changed from the normal condition is proved by the accumulation of material in the tracheids and medullary ray cells influenced by the presence of the fungi. The nature of these accumulated substances has already been discussed. Not only are the metabolic activities of the host cells altered, but the cambium in which the mycelia lives is stimulated to increased divisional activity, and this stimulation may exert itself to some distance. Townsend²⁸ has shown that "the influence of an irritation, due to cutting or other injury, is capable of acting through a distance of several hundred millimeters." It would seem, therefore, that plants that are victims to parasitic fungi may possibly be influenced as if they were wounded. How this increased activity of the host cells expresses itself in the increase in the amount of wood and bast has already been discussed. It appears that the fungi perennate in the wood of the canker, forming there a loose open reticulum, much like a coarse fish-net, and that they cause an alteration in the activities of the cells, obtaining for themselves thereby a sufficient amount of food for continued slow growth. The hyphæ which are instrumental in the formation of the swellings clearly reside in the wood cambium and adjacent soft bast cells, being able to draw upon the supplies of that part of the mycelium which has lived longest in the stem. It appears then that the mycelium of the wood was once as active as the mycelium of the cambium, and that as the permanent tracheids and medullary ray cells were formed the walls of the hyphæ increased

²⁸ TOWNSEND, The Correlation of Growth Under the Influence of Injuries, *Annals of Botany*, XI, pp. 509-532 (1897).

correspondingly in thickness, and maintained for some time a slow growth through the wood and medullary ray cells.

We have these changes in the structure and metabolism of the cells of white cedar paralleled by examples recorded by other botanists. Halsted²⁹ states that "one of the most striking instances of starch localization is found in the leaves of ordinary corn that are infested with the smut (*Ustilago maydis* D.C.). Pieces of leaves that were more or less distorted by nodules and projections of the smut-bearing tissue . . . were placed in the iodine, when the blue color began almost immediately to appear in the swollen tissue." Again: "An interesting study in this direction was made of the cedar galls of *Gymnosporangium macropus* Lk., where the starch is packed away in the enlarged host cells to their utmost capacity, and thin sections through the centres of the large galls display a neat fan-shaped appearance after they had been in iodine for a few minutes. The ordinary wood of the gall-bearing twigs show with the same treatment only a small amount of starch." Other cases of this influence of parasite upon host might be cited, but the illustrations mentioned above sufficiently show that in most instances the effect is a marked one, not only altering the chemical nature of the cell contents, but also the activity of the process of cell division with the formation of additional tissue elements.

TABULAR COMPARISON OF THE SEVERAL SPECIES OF THE GENUS GYMNOSPORANGIUM.

In the table on pages 498-501 an attempt is made to present the characters of the several species of the genus *Gymnosporangium*, so that a comparison of the structure of these fungi can readily be made.

SUMMARY.

1. The white cedar, *Cupressus thyoides*, is a stately tree, ranging from southern Maine to northern Florida and westward to Mississippi, and is not subject to any very serious disease.
2. There are nineteen species of fungi that live, saprophytically or parasitically, upon this tree.

²⁹ HALSTED, Starch Distribution as Affected by Fungi, *Bulletin of the Torrey Botanical Club*, XXV, p. 573.

3. Only two species of fungi, viz., *Gymnosporangium bisep-tatum* Ellis and *G. Ellisii* Berk., may be considered as serious parasites.

4. Historically these two funguses have been studied largely from a morphologic standpoint, and not from a physiologic or his-tologic point of view.

5. Wörnle and Tubeuf give the most satisfactory accounts of the several known species of *Gymnosporangium* and the diseases produced by them.

6. The two diseases are prevalent in the cedar swamps of New Jersey, where *Cupressus thyoides* makes an almost pure stand of timber.

7. Sections of the swellings caused by the fungi were made by means of a hand-plane and stained with aniline-green, Bismarck-brown, and a double stain consisting of methyl-green and acid-fuchsin.

8. The swellings produced by *Gymnosporangium bisep-tatum* are usually nodose, increasing year by year, until they may be brain-like in appearance and six to eight inches in diameter.

9. Those produced by *G. Ellisii* are never so thick, but the branches involved radiate out in a fan-like manner, assuming the character and appearance of witches' brooms.

10. The normal stem structure is described as a means of throw-ing light upon the abnormal structures produced by the fungi.

11. The stem structure in general is that common to other conif-ers, but the resin canals are confined to the bast and cortex.

12. The number of tracheids produced normally in a radial line are set forth in tabular form, as an expression of the variation in size of the several annual rings.

13. The environmental conditions are shown to have considerable influence in determining the spread of the diseases.

14. Sphagnum bogs are cold because the winter cold persists well on into the summer.

15. This persistence of the winter cold retards the development of the tree each year until summer is well advanced, and this retardation, it is thought, is reflected in the uniformity in size of the tracheids, there being little well-marked autumn wood.

16. The retardation of growth, with the persistence of the winter's cold in the bog, also exerts an appreciable influence on the growth of the parasitic fungi, which cause the canker-like swellings on the white cedar.

17. It is assumed that the perennial habit and slow growth of the mycelia are direct expressions of the inhibitory effect of the cold environment.

18. In considering the pathological transformations, a comparison is instituted with the disease produced by *Dasyceypha resinaria* in *Abies balsamea*.

19. By means of a table it is shown that the number of tracheids in a swelling produced by one of the fungi is vastly greater than in a normal stem of the same age.

20. The increased activity of the phellogen is also a marked feature of the disease due to *Gymnosporangium bisepatum*.

21. Several additional well-marked layers of cork are laid down as a result of this activity of the cork cambium.

22. As the disease progresses these cork layers begin to slough off.

23. The formation of the excrescences through the death of the cambium in part, and the attempt made on the part of the host to repair the damage are minutely described.

24. Pathological changes in the wood due to *G. bisepatum* result in the plugging of the tracheids and the final cracking of the sapwood when the parasitic attack has been long maintained.

25. The number of plugged tracheids is shown by an enumeration to be extremely variable in the several annual rings of wood.

26. The material filling the plugged tracheids in the disease caused by *G. bisepatum* is supposed to be fungus gamboge, from a number of chemical reactions obtained for the purpose of deciding this question.

27. Resin is also present in the most diseased areas, as determined by the copper acetate (Unverdorben-Franchimont) reaction.

28. The mycelium of *G. bisepatum* is described as a loose net. The hyphæ penetrate the wood, cambium and phlœm cells, spreading longitudinally and horizontally.

29. The hyphæ in growing from tracheid to tracheid take advantage of the bordered pits, the middle lamella of which disappears by ferment action.

30. The relation of the hyphæ to the host cells is carefully described.

31. The mycelium of *G. Ellisii* is more copious than that of *G. bisepatum*. It also grows through the cortex, bast and wood.

32. The hyphæ of this fungus are characterized by the ventricose swellings produced, and by the fact that they grow into the intercellular spaces of the brown patches of diseased tissue formed in the wood.

33. The hyphæ of *G. Ellisii* grow through the lumen of the tracheids and from tracheid to tracheid by means of the bordered pits, much as in the other fungus described.

34. The distribution of the tracheids containing hyphæ is presented in tabular form.

35. The pathological conditions induced by *G. Ellisii* are more severe at first than those caused by *G. bisepatum*.

36. Patches of diseased tissue are found in the stems of white cedar as brown spots of a wedge shape. These brown areas become more or less confluent until they may involve the circumference of the stem. Into these brown patches the hyphæ grow.

37. An enumeration of the tracheids in the diseased branches is also presented in tabular form, as a means of comparing the size of normal and diseased stems.

38. The belief is expressed, in conclusion, that the fungi cause marked metabolic changes in the stem, accompanied by the accumulation of resins and other substances, products of increased cell activity.

39. A tabular comparison of the several species of the genus *Gymnosporangium* is presented to show the relationship of the fungi studied to other species of wide distribution.

40. The bibliography details the papers consulted in the preparation of this paper by the writer.

| Name of Fun- gus. | <i>Gymnosporangium conicum</i> D. C. (<i>G. juniperinum</i> Winter.) | <i>Gymnosporangium fuscum</i> D. C. (<i>G. sabinæ</i> Winter.) | <i>Gymnosporangium Elisii</i> Berk. | <i>Gymnosporangium clavipes</i> Cooke and Peck. |
|------------------------|---|---|---|--|
| Host Plants. | <i>Juniperus nana</i> , <i>Juniperus communis</i> , <i>Juniperus virginiana</i> . | <i>Juniperus virginiana</i> , <i>Juniperus communis</i> , <i>Juniperus sabinæ</i> , <i>Juniperus oxycedrus</i> . | <i>Cupressus thyoides</i> . | <i>Juniperus virginiana</i> . |
| Habit of Fun- gus. | Long swellings in the branches. | Causing long swellings of the branches. | Fan-shaped fasciculation distorting the smaller branches. | Leaves and branches producing nest-like distortions. |
| Duration of Mycelium. | Perennial. | Perennial. | Perennial. | Perennial? |
| Host Tissues Infected. | Tissues of the branches. | Wood and less frequently in the medullary rays. | Medullary rays forming partial circles in the annual rings. Largely in the cambium. | Leaves. Tissues swell to twice original size. |
| Character of Mycelium. | Much branched, somewhat knotted or balled. | Fine hyphæ, little branched, running up and down and in toward the center of the stem. | Collected in brownish spots. Extends along the branches a distance of 18 inches. | Abundant. |
| Sporiferous Masses. | Subpyriform, or indefinitely expanded. Orange colored. $\frac{1}{2}$ inch high. | Numerous, approximated, brownish when dry, dark orange when swollen. $\frac{1}{4}$ – $\frac{1}{2}$ inch high. | Numerous, cylindrical, filiform. Orange colored. $\frac{1}{4}$ inch high. | Subpyriform, irregularly globose, then indefinitely expanded. Orange. $\frac{1}{4}$ inch high. |

| | | | | |
|--|--|---|---|--|
| <i>Gymnosporangium nidus-avis</i> Thaxter. | <i>Gymnosporangium clavariæforme</i> D. C. | <i>Gymnosporangium bisepatum</i> Ellis. | <i>Gymnosporangium globosum</i> Farlow. | <i>Gymnosporangium macrosporus</i> Lk. |
| <i>Juniperus virginiana</i> . | <i>Juniperus communis</i> . | <i>Cupressus thyoides</i> , <i>Libocedrus decurrens</i> . | <i>Juniperus virginiana</i> . | <i>Juniperus virginiana</i> . |
| Leaves, branches and trunks producing bird's nest distortions. | Branches causing long fusiform swellings. | Stems and branches forming large and small nodose swellings. | Smaller branches producing globose swellings. | Attacking leaves and smaller twigs and producing spherical reddish swellings. |
| Perennial. | Perennial. | Perennial. | Perennial. | Annual. |
| Tissues of leaves, branches, trunk. | Wood forming a rim in the annual growth, frequently in the medullary rays. | Cam bium, wood and medullary rays. | Tissues of stem and leaves. | Cells of leaves. |
| | Fine hyphæ, little branched, growing up and down and inward. | Hyphæ large, brown, branched to form a reticulum. | Abundant. | Abundant, producing haustoria which grow into leaf cells. |
| When young cushion-like, irregularly globose or oval, small and distinct or elongate and confluent, rich red-brown; moist and swollen, orange colored. | Numerous, scattered or aggregated, bright yellow when swollen. | Flattened and brownish when dry, hemispherical, yellow and rugose when swollen. | Globose, densely aggregated, dark brown when dry, yellowish-orange when swollen. $\frac{1}{4}$ – $\frac{1}{2}$ inch high. | Aggregated in globose masses, orange-yellow, cylindrical, gelatinous. $\frac{1}{2}$ –1 in. long. |

| Name of Fungus. | <i>Gymnosporangium conicum</i> D. C. (<i>G. juniperinum</i> Winter.) | <i>Gymnosporangium fus-cum</i> D. C. (<i>G. sabinae</i> Winter.) | <i>Gymnosporangium Elisii</i> Berk. | <i>Gymnosporangium clavipes</i> Cooke and Peck. |
|--------------------------|---|---|---|---|
| Teleutospores. | 15-18 μ diam., 48-58 μ long, two-celled, constricted at septum. | 15-22 μ diam., 38-53 μ long, two-celled, constricted at septum. | 10-16 μ diam., 75-190 μ long, three to four- celled, some- times one to five-celled. | 22-38 μ diam., 40-60 μ long, two-celled, constricted at septum. |
| Name of Ræstelia. | <i>Ræstelia cornuta</i> (Gmel.) Fr. | <i>Ræstelia cancellata</i> (Jacq.) Rebent. | <i>Ræstelia transformans</i> Ell. | <i>Ræstelia aurantiaca</i> Pk. |
| Intermediate Hosts | <i>Sorbus aucuparia</i> , <i>Sorbus aria</i> , <i>Cydonia vulgaris</i> , <i>Amelanchier canadensis</i> , <i>Pirus malus</i> , etc. | <i>Cratægus oxyacantha</i> , <i>Pirus communis</i> . | <i>Pirus malus</i> , <i>Pirus arbutifolia</i> . | <i>Pirus malus</i> , <i>Pirus arbutifolia</i> , <i>Amelanchier canadensis</i> , |
| Geographic Distribution. | Massachusetts, New York, South Carolina, Northern and Central Europe. | Massachusetts, Maryland, Europe. | Massachusetts, New Jersey. | E. Massachusetts, New York, New Jersey, Pennsylvania, North and South Carolina. |

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| <i>Gymnosporangium nidus-avis</i> Thaxter. | <i>Gymnosporangium clavariæforme</i> D. C. | <i>Gymnosporangium bisepitatum</i> Ellis. | <i>Gymnosporangium globosum</i> Farlow. | <i>Gymnosporangium macrosporus</i> Lk. |
| .055 x .025 μ , two-celled. | 13-19 μ diam., 55-90 μ long, two-celled. | 15-20 μ diam., 50-84 μ long, two to six-celled, or three to four-celled. | 19-21 μ diam., 38-45 μ long, two-celled. | 15-20 μ diam., 45-60 μ long, two-celled, constricted at septum, with papilla at each end. |
| <i>Ræstelia nidus-avis</i> Thaxt. | <i>Ræstelia lacetrata</i> (Sow.) Mer. | <i>Ræstelia botryapites</i> Schw. | <i>Ræstelia lacetrata</i> 2 (Thaxter). | <i>Ræstelia pyrata</i> (Schw.) Thaxt. |
| <i>Cydonia</i> (quince), <i>Amelanchier canadensis</i> . | <i>Pirus communis</i> , <i>Crataegus oxyacantha</i> , <i>Crataegus grandiflora</i> , <i>Crataegus sanguinea</i> , <i>Crataegus nigra</i> , etc. | <i>Crataegus tomentosa</i> , <i>Amelanchier canadensis</i> . | <i>Crataegus coccinea</i> , <i>Pirus americana</i> , <i>Pirus malus</i> , <i>Cydonia</i> (quince; pear), <i>Amelanchier canadensis</i> . | <i>Crataegus tomentosa</i> , <i>Crataegus Douglasii</i> , <i>Amelanchier canadensis</i> , <i>Pirus malus</i> , <i>Pirus coronaria</i> , <i>Pirus arbutifolia</i> . |
| Connecticut. | Maine, Connecticut, Northern and Central Europe. | Massachusetts, New Jersey and California. | Massachusetts to South Carolina. | Massachusetts to South Carolina, west to Missouri, Colorado, Wisconsin. |

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EXPLANATION OF PLATES XXII AND XXIII.

Figs. 1, 2, 3, 4, 5.—Abnormal swellings on the white cedar (*Cupressus thyoides*) caused by mycelium of fungus, *Gymnosporangium biseptatum*.

Fig. 6.—Larger gnarled, diseased condition of the branches of white cedar produced by *G. Ellisii*.

Fig. 7.—Small swelling on twig of white cedar produced by the mycelium of *G. biseptatum*.

Fig. 8.—Straight witches' broom produced by the perennial mycelium of a fungus, *Gymnosporangium Ellisii*.

Fig. 9.—Normal tracheids of white cedar in transverse section.

Fig. 10.—Cambium and adjacent cells from a normal stem.

Fig. 11.—Normal resin canal from bark of white cedar, showing resin.

Fig. 12.—Medullary ray cells and tracheids from a small abnormal swelling, such as the photograph depicted in fig. 7.

Fig. 13.—Diseased wood and excrescence on a young stem of white cedar.

Fig. 14.—Same section viewed entire. The depressed areas represent spots where the cambium has been killed.

Fig. 15.—Medullary ray cell from a longitudinal section, showing appearance of brown contents.

Fig. 16.—Tracheids filled with material under the stimulation of the mycelium of *G. biseptatum*.

Fig. 17.—Tracheids situated between two medullary ray cells, showing those plugged with fungus gamboe.

Fig. 18.—Cambial cells and outer wood tracheids, showing the presence of hyphæ in cross-section.

Fig. 19.—The same much enlarged.

Fig. 22.—Tracheids and medullary ray cells from the wood of white cedar, showing the course of the horizontal and longitudinal hyphæ.

Fig. 23.—Medullary ray cells, illustrating the manner in which a hypha penetrates the cell wall.

Fig. 24.—Section of stem diseased by the presence of fungus, *Gymnosporangium Ellisii*. The course of the hyphæ from tracheid to tracheid is shown. The hyphæ in several places are seen to grow through the bordered pits.

Fig. 24a.—Course of a hypha which grows through the bordered pits. Notice that the hyphæ become lens-shaped in the cavity of the bordered pit. *G. Ellisii*.

Fig. 25.—Hypha enlarged, showing the nodose or ventricose enlargement of the fungal cells. *G. Ellisii*.

Fig. 26.—Details of hypha of *G. Ellisii*.

Fig. 27.—The same from the wood.

Fig. 28.—Bent and twisted hyphæ growing in the brown areas of broken-down tissue, as shown also in fig. 29.

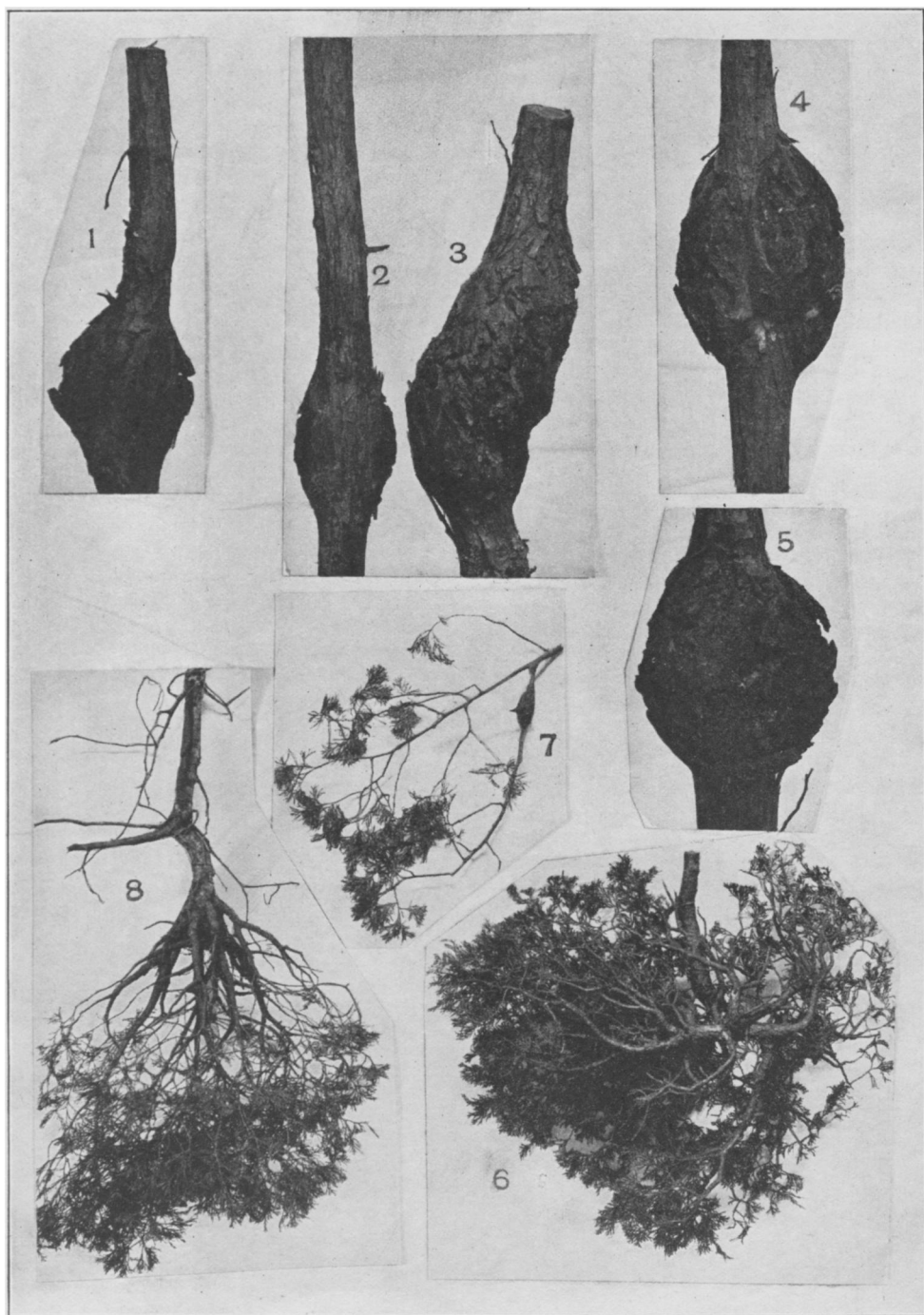
Fig. 29.—Spores (several forms) of *Gymnosporangium biseptatum* (after Tubeuf).

Fig. 30.—Spores (uni- and multicellular) of *G. Ellisii* (after Tubeuf).

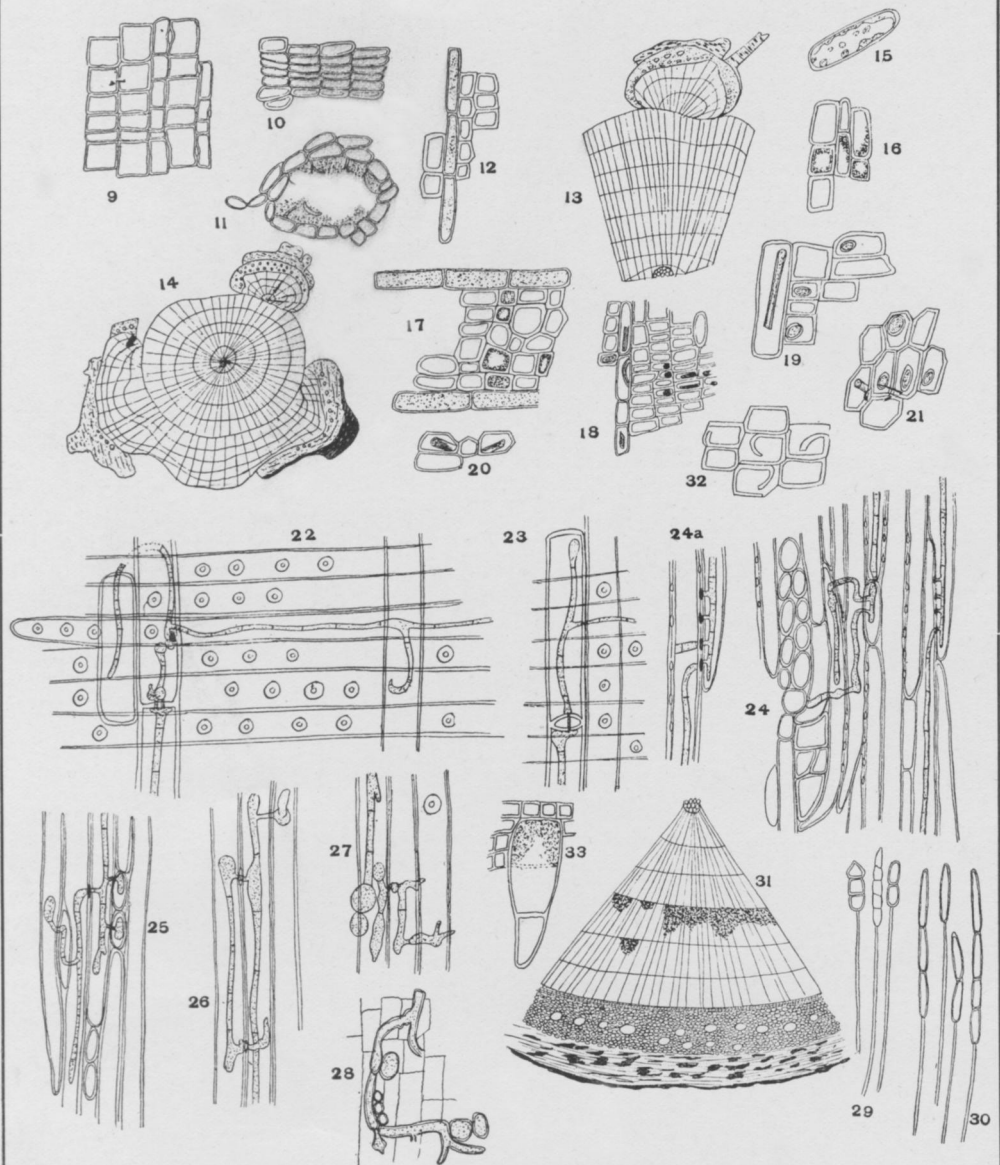
Fig. 31.—Transverse section of diseased white cedar stem, showing the diseased brown areas in the wood which have become more or less confluent.

Fig. 32.—Tracheids from diseased wood of white cedar, showing the sprung lignified cell wall.

Fig. 33.—Commencement of brown wedge-shaped areas of diseased tissue. Notice the abnormal size of the cells filled with granular matter.



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